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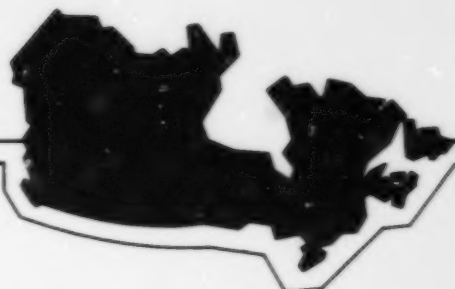
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Growth, survival, and stem form of a 22-year-old Norway spruce progeny test

M.N. Coleman, T.C. Neiman, and T.J. Boyle

Information Report PI-X-73
Petawawa National Forestry Institute



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**GROWTH, SURVIVAL, AND STEM FORM OF A 22-YEAR-OLD
NORWAY SPRUCE PROGENY TEST**

Information Report PI-X-73

M.N. Coleman¹, T.C. Nieman, and T.J.B. Boyle

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de la tige des individus de 22 ans d'épinette
de Norvège soumis à un test de provenance.**

Contents

<i>i</i>	Abstract/Résumé
1	Introduction
2	Materials and methods
5	Results
7	Discussion
8	Conclusions
8	References

Tables

2	1. Seedlot origin
4	2. ANOVA table with Expected Mean Squares (EMS) and F-statistic construction
6	3. Group means (standard errors in parentheses)
6	4. Heritability of height, diameter, and height/diameter ratio

ABSTRACT

Measurements of height and diameter and ratings of weevil (Pissodes strobi) damage to stem form in a 22-year-old progeny test of Norway spruce (Picea abies (L.) Karst) were combined with previous assessments of spring frost damage and parental weevil damage to estimate heritabilities for several variables. Limitations of experimental design complicated interpretation, but heritabilities of growth variables were typical of those estimated for other conifer species. Genetic control of tolerance to weevil attack appears to be high. Volume increment exceeded that of the best local white spruce (Picea glauca (Moench) Voss) plantations.

RÉSUMÉ

Les auteurs ont mesuré la hauteur et le diamètre d'épinettes de Norvège (Picea abies [L.] Karst) âgées de 22 ans et soumis à un test de provenance. Les classes des dommages à la forme de la tige, dus au charançon (Pissodes strobi), ont été déterminées. Afin d'estimer l'héritabilité de certaines variables, ces données ont ensuite été combinées aux résultats des évaluations antérieures des dégâts causés par la gelure printanière et des ravages provoqués chez les parents par le charançon. Les limites du plan d'expérience ont rendu l'interprétation des données plus difficile, mais l'héritabilité des variables relatives à la croissance correspondait à la plage des valeurs estimées chez d'autres essences de conifères. La régulation génétique de la tolérance aux invasions du charançon semble élevée. Leur vitesse d'accroissement en volume était supérieure à celle des meilleures plantations locales d'épinettes blanches (Picea glauca [Moench] Voss).

GROWTH, SURVIVAL, AND STEM FORM OF A 22-YEAR-OLD NORWAY SPRUCE PROGENY TEST

INTRODUCTION

Norway spruce (*Picea abies* (L.) Karst), native to central and northern Europe, has been widely planted as an exotic in North America. On appropriate sites, some provenances of Norway spruce grow exceptionally well in comparison with local white spruce (Holst 1955; Teich 1972; Fowler and Coles 1979; Fogal et al. 1980; Park et al. 1981; Jokela et al. 1986). For this reason, genetic improvement and selection programmes have been established for Norway spruce in various regions of eastern Canada (Corriveau et al. 1986; Lamontagne 1986; Mullin and Frame 1986; Rauter and Stubbart 1986; R. Wasser, pers. comm.). However, the species tends to suffer extensively from both winter freezing damage, associated foliage dessication, from spring frost damage on some sites, and also from stem deformation caused by the white pine weevil (*Pissodes strobi*).

Physiologically, cold causes damage to plant cells either through intracellular freezing, causing rupture of the cell wall and death of the tissue, or through intercellular freezing, associated with diffusion of water out of the cells and consequent dehydration (Siminovitch et al. 1967). Seasonally decreasing temperatures result in increased cold tolerance of plant cells (Siminovitch et al. 1967). Rapid falls in temperature, associated with late spring or early autumn frosts, cause intracellular freezing in newly formed, cold intolerant cells, for example in expanding buds and active cambial tissue. Conversely, slowly falling temperatures lead to intercellular freezing and the survival of the tissue depends on its ability to survive dehydration. There is abundant evidence for genetic variation in winter hardiness and frost tolerance (Holzer 1969; Eriksson et al. 1978; Dormling 1982) related to environmental variables such as latitude and elevation of the seed sources and test sites.

Adult white pine weevils burrow into the leading shoot to both feed and oviposit (Sullivan 1961). Such damage can result in death of the leading shoot, with one or more of the laterals in the whorl immediately below subsequently taking over as a leader. Weevil tolerance can take the form of avoidance of attack, tolerance of damage to the leader, or the development of a single lateral into a leading shoot without associated loss of vigour or stem form.

Some of the oldest experimental plantations of Norway spruce in North America were established at the Petawawa National Forestry Institute (PNFI). Results are presented from one such test designed to (1) compare growth of Norway spruce progeny of different parents, (2) investigate differential susceptibility to white pine weevil, and (3) examine the long-term effect of spring frost damage. Further, local white spruce (*Picea glauca* (Moench) Voss) plantations allow a comparison to be made of the relative productivity of the two species.

MATERIALS AND METHODS

In 1924, a plantation of 1500 Norway spruce was established at the Petawawa National Forestry Institute on abandoned farmland known as Hudson's Place. The plant material was obtained from a paper company in Québec and it is believed to be of Central European, possibly German, origin. After an extremely severe winter in 1933-34 the plantation was heavily rogued. Most of the trees which were not winter-hardy were removed, the majority of which had been killed above the snow-line by the low temperatures. By 1961 only 29 of the original trees remained.

In 1963, open-pollinated seed was collected from four trees at Hudson's Place and also from four clones of Hudson's Place material. In addition, control-pollinations carried out in 1962 yielded seed from five full-sib families (Table 1).

In 1967, 2 + 2 seedling stock from these 13 seedlots were outplanted in eight groups based on female parents (Table 1) at PNFI. A total of 1167 seedlings were planted in three replicates at 1.8 x 1.8 metre spacing with variable plot size. Randomization within blocks was on the basis of groups (seed parents); seedlots from the same group were planted in adjacent plots. Of the eight seed parents, four (numbers 98, 102, 115, and 119) had been selected in 1934 as completely winter hardy and three (numbers 100, 109, and 122) were assessed in 1961 to be weevil resistant. Tree number 98 was classed as being weakly weevil resistant and the remaining four seed parents were considered non-resistant.

Table 1. Seedlot Origin

Seedlot No.	Origin	Group	No. Plants
S4011-63	St. 98 X St. 99	I	28
S4012-63	St. 98 X St. 102	I	90
S4013-63	St. 98 open poll.	I	150
S4022-63	VC. 98 open poll.	I	150
S4016-63	St. 99 open poll.	II	150
S4017-63	St. 100 X St. 109	III	90
S4018-63	St. 100 open poll.	III	150
S4019-63	St. 109 X St. 100	IV	120
S4020-63	St. 109 open poll.	IV	149
S4021-63	St. 122 X St. 116	V	15
S4023-63	VC. 115 open poll.	VI	30
S4024-63	VC. 119 open poll.	VII	24
S4025-63	VC. 102 open poll.	VIII	21
			1167

St. = Seed Tree

VC. = Vegetative Propagule (graft) of selected tree

In 1972, at an age of nine years from seed, spring frost damage was assessed according to the following scale:

- 0: late flushing or no frost damage
- 1: leading shoot undamaged, lateral shoots "lightly" damaged
- 2: leading shoot undamaged, lateral shoots "heavily" damaged
- 3: only leading shoot damaged
- 4: leading shoot and laterals "lightly" damaged
- 5: leading shoot and laterals "heavily" damaged

In 1986, heights and diameters were recorded and an assessment made of stem form. Included in this assessment was the presence or absence of a forked stem below 60 cm height, believed to be caused by frost damage to the juvenile leading shoot. Frost damage could result in more than a single lateral shoot taking over as leader. Whereas frost damage is more likely on young trees, serious weevil attack tends to occur on trees greater than 1 m in height. The degree of apparent weevil damage, based on the following criteria, was also assessed.

<u>Number of stem deformations</u>	<u>Severity of deformations</u>
0: no deformations	1: Excellent recovery - negligible deformation
1,2,3: one, two, or three deformations	2: Deformation $\leq$ diameter at point of damage
4: $\geq$ four deformations	3: Deformation $>$ diameter at point of damage

Due to imbalance in mating design and non-randomization of families within the seed parent, the analyses of variance for heights and diameters were performed using the model:

$$Y_{ijk} = \mu + \text{rep}_i + \text{group}_j + \text{rep} \times \text{group}_{(ij)} + e_{ijk}$$

where

Y_{ijk} = observation of the kth progeny from the jth group in the replication

μ = common mean

rep_i = effect of ith replication

group_j = effect of jth group (i.e. seed parent)

$\text{rep} \times \text{group}_{(ij)}$ = jth group effect within the ith replication

e_{ijk} = environmental and remainder of genetic deviations

An ANOVA table was constructed as shown in Table 2. Due to the unbalanced nature of the plot design, a group component of variance within the replication source of error ($b \neq 0$) is to be expected. However, the degree of imbalance was so small that b was considered to be negligible.

Table 2. ANOVA table with Expected Mean Squares (EMS) and F-statistic construction

Source	DF	EMS	F-value
Replication	i-1	$\sigma_e^2 + a\sigma_{rxg}^2 + b\sigma_g^2 + c\sigma_r^2$	MS(r)/MS(rxg)
Group	j-1	$\sigma_e^2 + d\sigma_{rxg}^2 + f\sigma_g^2$	MS(g)/MS(rxg)
Rep x Group	(i-1)(j-1)	$\sigma_e^2 + \sigma_{rxg}^2$	MS(rxg)/MS(e)
Error	ijk-1	σ_e^2	MS(rxg)/MS(e)

Variance components due to replications (σ_r^2), groups (σ_g^2), replication x group interaction (σ_{rg}^2), and residual within-plot error (σ_w^2) were calculated. Height, diameter, and height/diameter ratio heritabilities were estimated using the following formulae:

$$\text{single tree heritability } h_{ST}^2 = k\sigma_g^2 / (\sigma_g^2 + \sigma_{rg}^2 + \sigma_w^2)$$

$$\text{family heritability } h_F^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{rg}^2 / r + \sigma_w^2 / nr)$$

where k = constant (see below)

σ_g^2 = group variance

σ_{rxg}^2 = rep x group variance

σ_w^2 = within plot variance

h = harmonic mean (= 11.2)

r = number of replications

For single tree heritability the constant k is determined by the genetic covariance among members of families or groups (Squillace 1974). For true half-sibs, this coefficient is equal to 4, as σ_g^2 accounts for $\frac{1}{2}\sigma_A^2$. Due to a finite number of pollen parents, half-sibs are likely to include samples of various full-sib families. Therefore, a value of k less than 4 is usually considered more realistic for open pollinated families. The value of k for full-sib families equals one-half of the additive genetic variance accounted for in the group variance. Assuming k equals 3.5 for open-pollinated families and 2.0 for full-sib families, the average value of k is determined by calculating the proportion of full-sibs in the test:

$$k = 3.5 - (297/959 \times 1.5)$$

$$= 3.04 = 3.0$$

Although k will vary among groups, the resulting adjustment required to account for this variation was considered unlikely to substantially affect heritability estimates.

RESULTS

Heights, diameters, height/diameter ratios, weevil damage rating, and survival are summarized by groups in Table 3. Mean height at age 22 from seed was 8.3 m and mean diameter was 10.5 cm. Dominant height, i.e. the mean height of the tallest 10% of the trees, was 10.3 m.

Differences among groups were significant for height and height/diameter ratio at the 1% level, but for diameter, the differences were only significant at the 5% level. For survival there were no significant differences among groups, nor were there significant differences among replications for any of the variables. The replication $\times$ group interaction was only significant for height growth (at the 5% level).

Single tree and family heritabilities were calculated for height, diameter, and height/diameter ratio (Table 4). For all three variables, single tree heritabilities were considerably less than family heritabilities, thus emphasizing the benefit of progeny testing in the selection of superior genotypes.

Because weevil susceptibility ratings yielded non-continuous and non-normal data, an analysis of variance is not valid, so an estimate of heritability of weevil susceptibility cannot be calculated from variance components in the normal way. However, ratings of parental susceptibility were available to allow the calculation of a parent-progeny regression. In the case of a regression of progeny means on single-parent values, the standard partial regression coefficient (b') estimates one half the narrow sense heritability (Falconer 1983). Parent-progeny regressions for deformation number and deformation severity yielded heritability estimates of 1.65 (0.11) and 1.60 (0.10), respectively (standard errors in parentheses).

Correlations of the 1972 frost damage rating with height, diameter, frequency of forked stems below 60 cm, and severity of stem deformation were all non-significant. However, the correlation with number of stem deformations was significant at the 1% level, although the actual magnitude of correlation was low (0.18).

Two pairwise comparisons are also of interest, namely a comparison of the reciprocal crosses between ST.100 and ST.109 and a comparison of the open-pollinated seedlots from ST.98 and VC.98 (ramets of the clone whose ortet was ST.98). Not surprisingly differences in height between the two reciprocals were negligible and non-significant (difference = 0.33 m; $t = 1.7$, 165 df). On the other hand, the difference in height growth between ST.98 and VC.98 was highly significant (difference = 1.29 m; $t = 6.42$, 223 df $P_{t=0} \leq 0.01$).

Table 3. Group means (standard errors in parentheses)

group	N	height (m)	diameter (cm)	height/diameter	no. deformations	deform. degree	survival (%)
I	325	7.90 (0.95)	10.3 (0.15)	7.94 (0.08)	2.08 (0.06)	2.33 (0.03)	80.1
II	138	8.65 (1.16)	10.4 (0.21)	8.65 (0.14)	2.03 (0.10)	2.12 (0.05)	92.0
III	204	8.65 (0.92)	10.8 (0.15)	8.39 (0.09)	1.63 (0.07)	2.07 (0.04)	85.0
IV	212	8.70 (0.84)	11.0 (0.14)	8.12 (0.09)	1.71 (0.08)	1.92 (0.04)	86.9
V	13	6.98 (5.81)	8.2 (0.86)	8.76 (0.38)	1.76 (0.32)	1.92 (0.17)	86.7
VI	24	7.79 (2.12)	11.1 (0.37)	7.13 (0.24)	2.29 (0.22)	2.37 (0.11)	80.0
VII	23	7.60 (3.22)	10.7 (0.47)	7.19 (0.22)	2.08 (0.28)	2.21 (0.15)	95.8
VIII	20	8.75 (2.27)	11.1 (0.50)	8.13 (0.28)	1.85 (0.28)	2.40 (0.18)	95.2
Overall	959	8.38 (0.49)	10.6 (0.07)	8.16 (0.04)	1.89 (0.03)	2.15 (0.04)	84.9

Table 4. Heritability of height, diameter, and height/diameter ratio

parameter	type	h^2
height	single tree family	0.171 0.365
diameter	single tree family	0.166 0.457
h/d Ratio	single tree family	0.119 0.613

DISCUSSION

Estimates of heritability of height growth were comparable with other species (Zobel and Talbert 1984) and those from other studies in Norway spruce. Ekberg et al. (1985) estimated family heritability to be 0.24-0.26 for height growth of Norway spruce planted at four sites in Sweden at five years of age and for 9-year-old Danish Norway spruce, Wellendorf (1983) obtained an estimate of 0.44. Because the estimates from this experiment were obtained from a single plantation, they will, as a consequence, be inflated by a term for the family x site interaction (Dickerson 1963).

The need to carefully match seed source with site is particularly important for exotic species (Zobel and Talbert 1984). In the case of Norway spruce planted in continental climates of Canada, severe damage can be caused by late spring frosts, a lack of winter hardiness, or a combination of the two factors. Holzer (1969) found that frost tolerance in spruce is closely related to flushing time, which is under strong genetic control. Some of the parent trees in this progeny test had undergone mass selection for winter hardiness, but susceptibility to late spring frosts is not necessarily related to cold tolerance. Some frost damage did occur in the early years, but the lack of significant correlations with growth variables suggests that frost susceptibility and poor growth are not associated. Similarly, there appeared to be no association between frost damage to the leading shoot and frequency of forked stems. Teich (1972) argued that management strategies restricting plantations to sites that are less prone to frost would be more efficient than selecting for frost tolerance. Certainly, it is expected that genetically superior trees will be utilized primarily on the best sites and this consideration, combined with the evidence from this test, suggests that frost susceptibility need not be a cause for concern in planting Norway spruce, provided that reasonable care is taken in the choice of material.

Although the heritability estimates for weevil susceptibility are outside genetically possible bounds, reflecting the weakness of the parent-progeny regression approach, they nevertheless indicate strong genetic control of weevil tolerance in Norway spruce. The fact that progeny of the three seed parents classified as "resistant" had the lowest average number of deformations and severity of deformations is a strong indication of the high level of genetic control of weevil tolerance. The mechanism for weevil tolerance in both white pine (*Pinus strobus* L.) and Norway spruce is uncertain, although various studies on pine have suggested some influence of bark thickness (Kreibel 1954), leader thickness (Sullivan 1961), and resin quantity and chemistry (Santamour 1965). Perhaps more significant than weevil susceptibility is the ability to recover without major stem deformation. Again, this experiment indicates that selection for good stem recovery is likely to result in substantial benefits in wood quality.

The growth rate of the Norway spruce progenies compares very favourably with locally grown white spruce plantations. Stiell and Berry (1967) produced yield tables for white spruce plantations at PNFI. The yield table for the top site class (dominant height 50 feet at age 40) indicates a dominant height for white spruce of 9.14 m at age 20, and a total volume of 85.5 m³/ha, compared with 10.31 m and 107.5 m³/ha respectively for this Norway spruce plantation. Growth to age 22 is representative of Yield Class 18 (maximum Mean Annual Increment = 18 m³/ha/yr) for Norway spruce plantations in

the United Kingdom (Hamilton and Christie 1971). The economic rotation age of a yield class 18 Norway spruce stand is between 40 and 50 years of age for a non-thin regime and about 10 years later for a stand thinned at prescribed intensities (Forestry Commission 1978). Thus the results of this progeny test indicate the performance of Norway spruce and estimate heritabilities at close to half rotation age.

CONCLUSIONS

Although imperfect experimental design, both in terms of the mating design and incomplete randomization, complicated interpretation of the results, some important conclusions can nevertheless be drawn from this experiment.

Firstly, it is clear that cold-hardy Norway spruce can be very productive in eastern Canada, out-performing local plantations of white spruce. Prospects for genetic improvement of growth characters are similar to those for other species of conifer, with family selection based on progeny test results being a far more efficient approach than mass selection. In addition, selection for tolerance to, or at least good recovery from, weevil attack should be possible in order to improve stem form and therefore wood quality. On the other hand, provided some care is taken in site and seed source selection, the risk of adverse effects of spring frosts on subsequent growth and stem form is not great. Genetic improvement of Norway spruce should, therefore, concentrate on winter-hardiness, growth, and weevil tolerance/recovery.

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